I talked with him the day before his operation, from which he did not recover, and he said, "I will be glad to have this over so I can get back and be cured by the birds and the ferns." If there is a place somewhere in the skies reserved for God's Noblemen, I am sure Ralph Benedict will be found in the front row.

HEWLETT, LONG ISLAND, NEW YORK.

Two New Species of Ferns from the United States1

W. H. WAGNER, JR.

During the course of a broad survey of "problem" fern groups in the United States a number of novelties have turned up; many of these are hybrids which seem to be sterile and incapable of normal reproduction. However, the two ferns to be described below, although probably of hybrid origin, do possess mechanisms for reproduction by spores, and indeed form sizeable populations extending over wide ranges. Both are "critical" species, in the sense that they show close similarities to other well-known ferns, and that is probably the reason they were heretofore overlooked.

POLYSTICHUM

Holly ferns of the north temperate regions have always presented a confusing picture to general taxonomists, especially the species with divided leaflets. Part of the problem has been nomenclatural (Alston, 1940), part the tendency of early authors to collect practically all of the bipinnate species under one taxon, *Polystichum aculeatum* (L.) Roth (Christensen,

Research was conducted under NSF project GB-2025, "The evolutionary characters of ferns." I wish to acknowledge the curators of the following herbaria for lending necessary specimens: University of British Columbia (UBC), New York Botanical Garden (NY), Gray Herbarium (GH), U. S. National Museum (US), University of Washington (WTU), and Yale University (YU). Also the following persons contributed suggestions and materials: H. E. Ahles, H. G. Baker, D. L. Branscomb, Thomas Darling, Jr., E. S. Ford, R. K. Godfrey, C. Leo Hitchcock, John D. Lovis, C. V. Morton, V. M. Morzenti, and Edgar T. Wherry.

1906, pp. 575-578; Copeland, 1947, p. 108), and part the apparently strong ability of the species of this genus to generate confusing hybrids (Manton and Reichstein, 1961; Meyer, 1959). It has long been known that the polystichums of the western United States involve a baffling series of populations. Of the more recent workers, Joseph Ewan (1942) has made some pioneering efforts to clarify their relationships. The following new species represents a "missing link" in the broad pattern of species relationships which will be discussed in a future paper.

Polystichum kruckebergii Wagner, sp. nov., Plate 1

Species P. scopulino similis sed foliis minoribus, pinnis magis triangularibus et magis profunde et acriter dentatis, dentibus paucioribus, venis primariis ex costa paucioribus, stipite saepe breviore vel fere nullo differt.

A small, tufted, stout fern of cool rocky places, with ca. b (2-11) leathery leaves and masses of densely packed stipes covering the rhizome to make its apparent diameter 2.2 (1.0-3.0) cm. Rhizome upright, up to 10 cm long, covered with matted roots below and with stipe bases above, the actual stem concealed in leaf armor, ca. 0.3-0.7 cm in diameter, occasionally forking. Scales of the stipe bases numerous, pale tan, essentially concolorous, 2-8 mm long, 1.0-2.5 mm broad, diminishing to much smaller size on the rachis. Fronds linear-lanceolate, 18.2 (8-30) cm long, 2.5 (1.3-4.0) cm broad, rigid and coriaceous, dark green and shiny, slightly paler and duller below, the lower pinnae narrowed to nearly sessile, the blade base with small more or less triangular pinnae, except in apparent shade or deep-crevice forms with stipes up to 10 cm long. Lamina provided with scattered, sparse glands. Stipes and lower rachises stout, drying to 1-3 mm thick, pale green or straw-colored. Rachis at first heavily scaly with reddish to pale whitish brown paleae 1.0 mm long or less and 0.5 mm wide or less, these deciduous in older leaves. Pinnae overlapping except in shade forms, mostly ovate-triangular, the median ones, 0.5-1.5 mm long, acute, and with well-developed anterior auricles. Pinnae margins with usually 4-8 conspicuous spreading, pointed teeth more or less tipped with short, hard bristles. Major veins usually ca. 6 (3-9) pairs from the leaflet axis. Sori submedial, in a single row on either side of the costa, except in luxuriant, deeply divided specimens with similar rows of sori on the pinnules. Sori usually becoming confluent at maturity, except

in shade forms. Indusium peltate with wavy margins. Sporangia bearing occasional paraphyses, these simple glands like those of the lamina, but borne on the capsules. Spores similar to those of P. scopulinum but with more rugose perispores (higher and more numerous crests) than those of P. mohri-

oides. Chromosomes n = 82 pairs.

Type: Trail to Mt. McLean at Lillooet, British Columbia, Canada, open grassy bank in opening in coniferous woods at 5100 ft., occasional locally, J. A. Calder 15550 and D. B. O. Savile, J. M. Ferguson (WTZ). Although the bulk of this species' range appears to be in the United States, this Canadian specimen was chosen to be the type because it shows the distinctive features more clearly than any other we have seen.

OTHER COLLECTIONS:

CALIFORNIA: SISKIYOU CO.: near Mt. Shasta, Lemmon in 1878 (UC—mounted on same sheet with P. mohrioides); TUOLUMNE CO., in deep rock crevice of metamorphics, s. slope Twin Peaks, head of Virginia Canyon, alt. 10,500 ft., Sierra Nevada, Edward Butts 192 (UC—very small, compact form); County?: mountains about the head waters of the Sacramento River, alt. 7500-8500 ft., C. G. Pringle in 1881 (NY).

OREGON: KLAMATH CO.: near Klamath Lakes, B. W. Evermann in 1897 (US); moist slopes, Pete's Point, Wallowa Mountains, alt. 2700 m., Morton E. Peck 18059 (WTU—mounted on same sheet with P. scopu-

linum); No data, T. J. Howell in 1882 (US).

WASHINGTON: YAKIMA CO.: crevices of rocks, Mount Adams, 6-7000 ft. alt., W. N. Suksdorf in 1882 (UC—specimen extremely lax, the pinnae of thin texture and widely spaced, apparently growing in deep crevice); W. N. Suksdorf in 1881 (US—2 sheets). PIERCE CO.: Mount Rainier, E. C. Smith 876 (WTU—2 sheets). CLALLAM CO.; a low spreading, stoutish fern growing in inaccessible crags beneath Obstruction Point, alt. 6,200 ft., Olympic Mountains, F. G. Meyer 1240 (US); Olympic Mountains, without definite locality, J. Nieman in 1932 (WTU—extremely small form); high alpine slope of Hurricane Ridge, 6500 ft., J. W. Thompson 14178 (WTU).

IDAHO: IDAHO CO.: on talus and in crevices above Sheep Creek Lakes #2, Dry Diggins area, Seven Devils Mountains, Nez Perce National Forest, 7500 ft., A. R. Kruckeberg 3192 (UC, NY); CUSTER CO.: crevices of high cliff near Stanley Lake, Challis National Park, Sawtooth Mountains, 8500 ft., J. W. Thompson 14039 (UC, NY).

UTAH: BOX ELDER CO.: infrequent dry places in crevices of cliffs, in contact with quartzite and serpentine, head of Middle Fork of Drum

²An additional specimen, *Henderson 1209* (US), is indicated as from "Mts. Adams and Hood," and thus is from either Washington or Oregon.

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POLYSTICHUM KRUCKEBERGII N. SP. TYPE SPECIMEN (WTU)

Canyon, 9500 ft., B. Maguire 2225 and A. H. Holmgren (US, UC, NY—the US collection shows the extremely lax, presumably "shade" condition, and that in NY includes an exceedingly small specimen roughly resembling a small Woodsia ilvensis).

BRITISH COLUMBIA: Elizabeth Mine, up Blue Creek, Lillooet Area, 6550 ft., B. F. Vrugtman 610767 (UBC); Creek from s. e. of Big Dog Mountain, Lillooet Area, 6600 ft., under rock in meadow above stream, Vrugtman 610661 (UBC); on serpentine rocks along Ladner Creek, 8-9 mi. in from Jessica, K. V. R., L. R. Harrison in 1944 (UBC); Bridge River Mountains, F. Perry in 1926 (UBC); Mount Moor, Middle Creek River, 7200 ft., W. Bird 3455 (UBC); Noaxe Lake, V. C. Brink in 1957 (UBC); summit ridge of Cadwallader Range, Bridge R. Mountains, 7000 ft., E. J. Grieg in 1954 (UBC).

Some idea of the past problems of identifying this species may be gained from examining the herbarium sheets cited above, and noting their most recent determinations. Of those which had been annotated, one was named "P. lemmonii," one as "P. mohrioides," 16 "P. scopulinum," and seven as "P. lonchitis." The newly described fern clearly resembles most closely the latter two species. ("P. lemmonii" and "P. mohrioides," the most finely divided taxa in this assemblage, are regarded by the present author as the same species.) Polystichum lonchitis is a circumboreal, very familiar species of fairly high latitudes (and altitudes in the western mountains); so far as I know, it is never so divided as to be bipinnate, as is P. kruckebergii. The problem is much greater in separating the new species from P. scopulinum.

Polystichum scopulinum (D. C. Eat.) Fern. was first designated as "Aspidium aculeatum var. scopulinum" (Eaton, 1880, p. 125). In checking the original description I found it completely insufficient to tell whether the type material of that taxon might not indeed be the fern described as new here. This possibility was increased by the fact that Eaton's original identification of his new "variety" was as "Aspidium lonchitis" (= Polystichum lonchitis). I therefore requested on loan its type specimen ("Herb. D. C. Eaton. Aspidium aculeatum ['lonchitis' had been erased, and 'aculeatum' written

over] Swz. var. scopulinum D. C. Eaton. Upper Teton Cañon, July 28. Hayden's Yellowstone Exped. 1872," YU) which was sent for my study by Dr. John Reeder, and is illustrated in *Plate 2*. The plant is definitely not *P. kruckebergii*; the long segments and general cutting are characteristic of what I have been treating as *P. scopulinum*.

For the diagnosis of the new species, I choose merely to compare it with P. scopulinum, the one species which I believe can cause the most serious difficulty. Polystichum scopulinum ranges widely in the mountains of western North America from New Mexico to British Columbia, and there is a remarkably isolated population of this fern on Mount Albert in Quebec. Evidently P. scopulinum is very much more common than P. kruckebergii. Typically P. scopulinum is a larger plant, and the pinnae are usually more oblong and longer (sometimes reaching over 4 cm.) than in P. kruckebergii. The number of marginal teeth and lateral veins per side of the median pinnae usually is about 12 (8-25) in P. scopulinum instead of approximately six in P. kruckebergii, thus reflecting the gross difference in pinna form. The pinna margins of P. scopulinum are not so bristly and the pinna tips are not so pointed as in P. kruckebergii. Also, P. scopulinum tends to have a longer stipe, this usually accounting for one-sixth to one-third of the length of the frond, and the series of "auricle-like" triangular pinnae which commonly run nearly to the leaf base in P. kruckebergii is lacking.

On the basis of our present knowledge we must conclude that the genetic relationships of the new species are with the complex of P. lonchitis, P. scopulinum, and P. mohrioides. A broader study of all western United States holly-ferns by the author (to be reported in the near future) leads to the hypothesis that P. kruckebergii is a species of hybrid origin between P. lonchitis and P. mohrioides, the two diploid species between which it is most nearly intermediate. Both of these presumed ancestors have n=41 chromosomes, but their intermediate, P. kruckebergii, has double that number, i.e., n=82, indicating

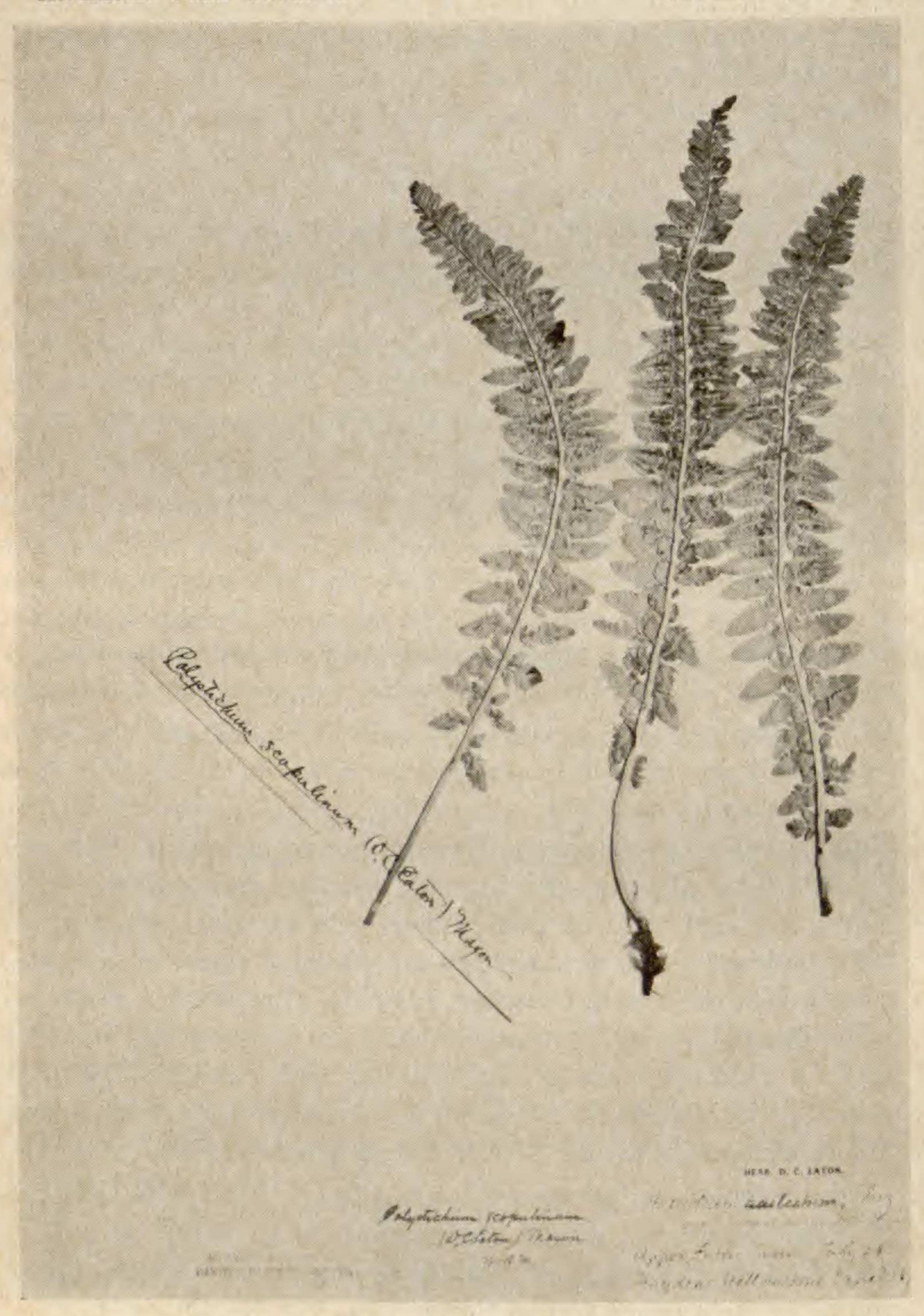
that the latter probably arose as an allotetraploid species from an originally sterile diploid hybrid, by spontaneous doubling of the chromosome complements. By the same token, P. scopulinum also proves to be morphologically intermediate between two diploids, and it is likewise a tetraploid with n=82. The resemblance of P. scopulinum to P. kruckebergii may be accounted for in part by their probable sharing of one ancestor, the diploid P. mohrioides. The other ancestor of P. scopulinum is evidently the diploid P. munitum (the abundant western "sword fern"), a species which resembles P. lonchitis to some extent, but which is clearly distinct. The characteristics by which P. munitum differs from P. lonchitis correspond to those in which P. scopulinum differs from P. kruckebergii, and thus confirms that the two species with divided leaves had different once-pinnate ancestors.

Polystichum kruckebergii evidently extends sporadically over a range from Utah and California north to British Columbia. It has been taken at altitudes as high as 10,500 ft. in California and as low as 5,100 ft. in British Columbia. The commonest habitat is in crevices in rock bluffs or talus, but the plant apparently favors colder and bleaker sites on the average than does P. scopulinum. Dr. Kruckeberg describes the Hurricane Ridge locality as follows: "The ferns are accessible with difficulty. The plant grows in rock fissures and crevices, high above the trail to Deer Park, about one-half mile northeast of Obstruction Point. It is well above the loose talus, on a northeast-facing rock wall of what must be Obstruction Point itself. The fern is not common, although it is practically the only fern in this otherwise botanically fruitful habitat. The only other fern present is Polystichum lonchitis—one lone plant about 50 yards to the north." (letter, August 3, 1963).

The new species is named for Professor Arthur R. Kruckeberg, in recognition of his contributions to its study, as well as his broad investigations of edaphic factors in the distribution of plants in the western United States.

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POLYSTICHUM SCOPULINUM (D. C. EATON) MAXON TYPE SPECIMEN (YU)

ASPLENIUM

Historically the Florida plant known as Asplenium heterochroum Kunze has been a source of confusion. Small (1938) wrote that the species was found in Florida 'perhaps as early as Asplenium resiliens, but was not distinguished from that plant until many years later." Long after the two species were distinguished, Roland M. Harper (1916) said that A. heterochroum is "Very similar to A. resiliens, . . . which has a similar habitat but much wider range." As late as 1935, the St. John brothers commented that some plants of A. resiliens "are hard to distinguish" from A. heterochroum. Nevertheless, the two species are distinct. Maxon (1913) discussed the group of Asplenium trichomanes and its American allies in some detail and distinguished 19 species in all, including the two under discussion. In regard to A. heterochroum he wrote (op. cit. p. 140), "From A. resiliens, with which it was long confused in Florida, it differs conspicuously in its chaff, which, though attenuate, is never hair-pointed, in the shape and position of its sori (these longer and much nearer the midvein), in its thin rather than decidedly coriaceous texture, and usually in the character of its margins. The reduced lower pinnae also are broadly cuneate and more or less flabelliform, never auriculate-cordate as in A. resiliens."

In view of the above it is interesting to recognize the fact, apparently overlooked until recently (Morzenti and Wagner, 1962), that there is a distinct species which is morphologically intermediate between A. heterochroum and A. resiliens. Evidence from range, morphology, and chromosomes indicates that this taxon probably arose as a hybrid between these two species, and the details of the evidence will be described in the near future by Miss Virginia M. Morzenti. The intermediate plant is capable of spore reproduction, and its geographical range extends beyond that of at least one of its parents. The recognition of this fern as a new species is based upon the fact that it becomes abundant in a number of localities (especially in Florida and North Carolina), it can reproduce independently,

and good specimens can be distinguished readily from either of the species with which it has previously been confused. The binomial to be proposed below was published as a nomen nudum (Wherry, 1964, p. 164), and the taxon was also listed as "Asplenium heterochroum × resiliens" (by Wagner, in Radford, Ahles, and Bell, 1964).

ASPLENIUM heteroresiliens Wagner, sp. nov., Plate 3

E gregis A. trichomanes, pinnis triangulari-ovatis vel oblongo-ovatis, inferioribus plus minusve descendentibus et saepe in latere postico leviter auriculatis, marginibus subintegris vel dentatis, laminis plus minusve firmis et coriaceis, venis soriferis furcatis supra auriculis basalibus saepe 1 vel 2, soris paullo supramedialibus, sporis magnis, ca. 40–50 μ longis, 32 per sporangium et sporis abortivis tamen paucis, chromosomatibus 180.

A member of the Asplenium trichomanes group, with triangular-ovate to oblong-ovate pinnae, the pinnae in the lower third of the frond somewhat descending and tending to form a low auricle on the posterior side of the base; pinna margins subentire to dentate; lamina somewhat firm and leathery; forked sorus-bearing lateral veins above the basal auricle usually 1 or 2; sorus slightly supramedial; normal spores large, ca. 40–50 μ long, 32 per sporangium but abortive spores also observed; chromosomes 180.

Type: About 5 miles northwest of High Springs, Columbia County, Florida, September 8, 1960, Ernest S. Ford (MICH). This complete specimen was kept as a living experimental plant at the University of Michigan Botanical Gardens (Accession no. 21689) and pressed on April 20, 1961. It served also as the voucher for chromosome observations. Fronds from this plant will be distributed to other herbaria).

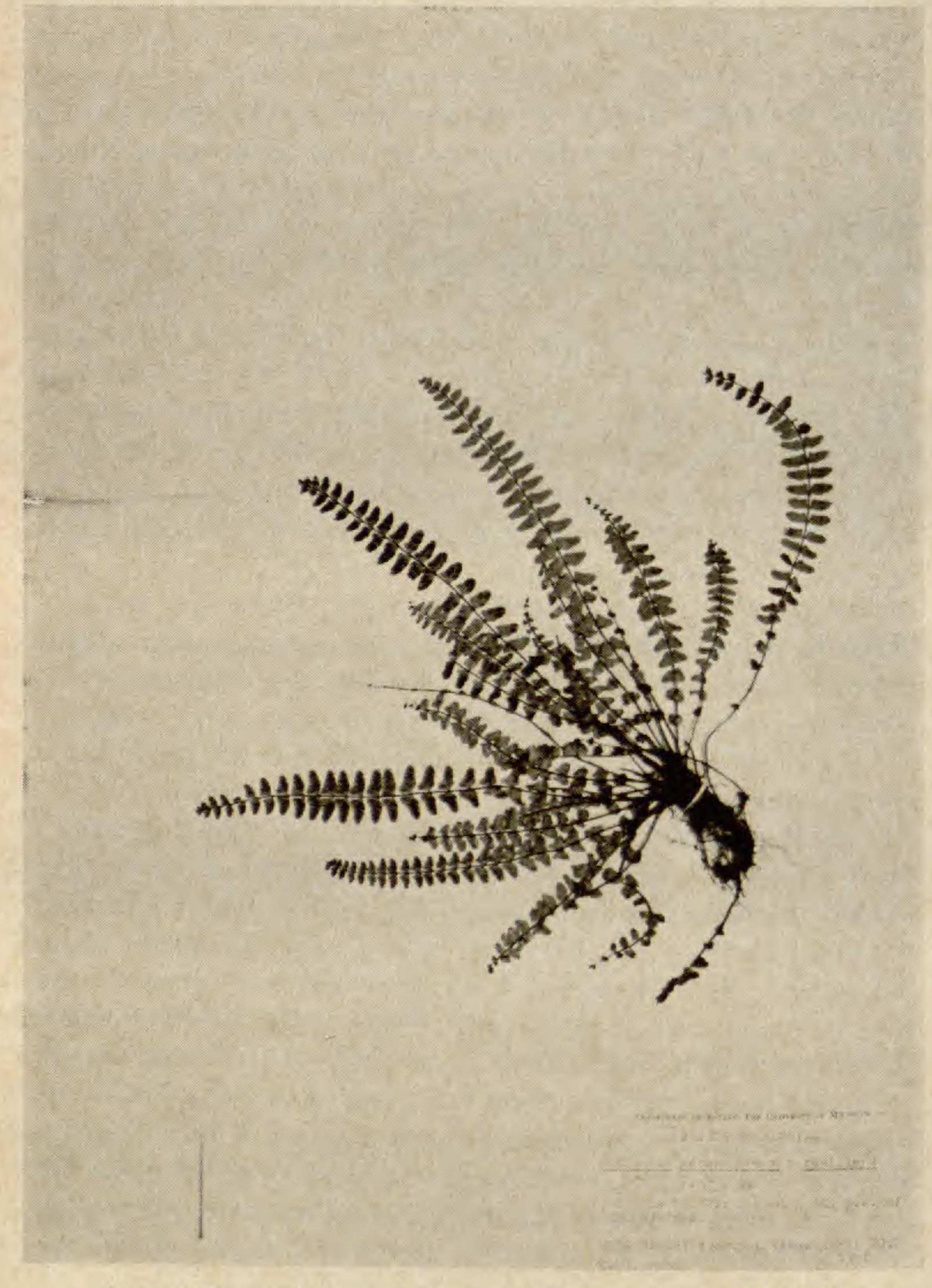
The diagnosis above should serve to bring out the salient characteristics of the plant. A lengthy taxonomic description is not called for here, because most of it would be a repetition of the characters familiar throughout the Asplenium trichomanes group. The most important and useful features for the recognition of A. heteroresiliens will be discussed below in terms of the corresponding features of its nearest relatives.

The pinna shape is intermediate between the nearly oblong pinnae of A. heterochroum in which the upper and lower margins are approximately parallel, and the more triangular-ovate ones of A. resiliens, the upper and lower margins converging toward the apex. The lower pinnae (i.e., in the lower third of the leaf) are somewhat descending as seen in dried specimens, not mostly perpendicular as in A. heterochroum, nor mostly descending as in A. resiliens. The pinna margins are variable, but they are usually shallowly dentate; they are only rarely as sharply crenate-dentate as in A. heterochroum, or as subentire or entire as in A. resiliens. Anterior (or upper) auricles are found at the pinna bases in all three ferns, but A. heteroresiliens shows a tendency to form in addition a slight posterior auricle also, especially in the basal third of the frond. In A. heterochroum a lower auricle is normally completely absent, but in A. resiliens it is normally present, and is sometimes nearly as prominent as the upper one.

The texture of A. heteroresiliens is firm and somewhat leathery, not so herbaceous as in A. heterochroum nor as coriaceous as in A. resiliens. One of the most useful distinguishing characters among these ferns involves the degree of forking of the veins, which may usually be observed directly in A. heterochroum but may need a drop of 70 per cent alcohol to be visible in thicker-textured plants. Usually the basal auricles of the pinnae show one or two vein furcations in all three ferns, so that the differences are seen in the sorus-bearing veins above the basal auricles. In A. heteroresiliens, a sample of 25 herbarium sheets (the largest frond examined on each) showed variation in number of sorus-bearing veins on the anterior side of the pinnae which were forked from 0 to 4. The average number of forked veins was 1.6. Corresponding observations of a sample of Florida A. heterochroum gave a range of 0 to 1, and an average of 0.3. In A. resiliens the veins show much more forking (and often a vein will fork twice); the sample of this species (all eastern U.S.) showed a range of 2 to 5, and an average of 3.6.

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ASPLENIUM HETERORESILIENS N. SP. TYPE SPECIMEN (MICH)

The sori of A. heteroresiliens are a little closer to the margin than the costa. The sori in these ferns must be compared in the largest and most ample fronds, for those which are dwarfed or

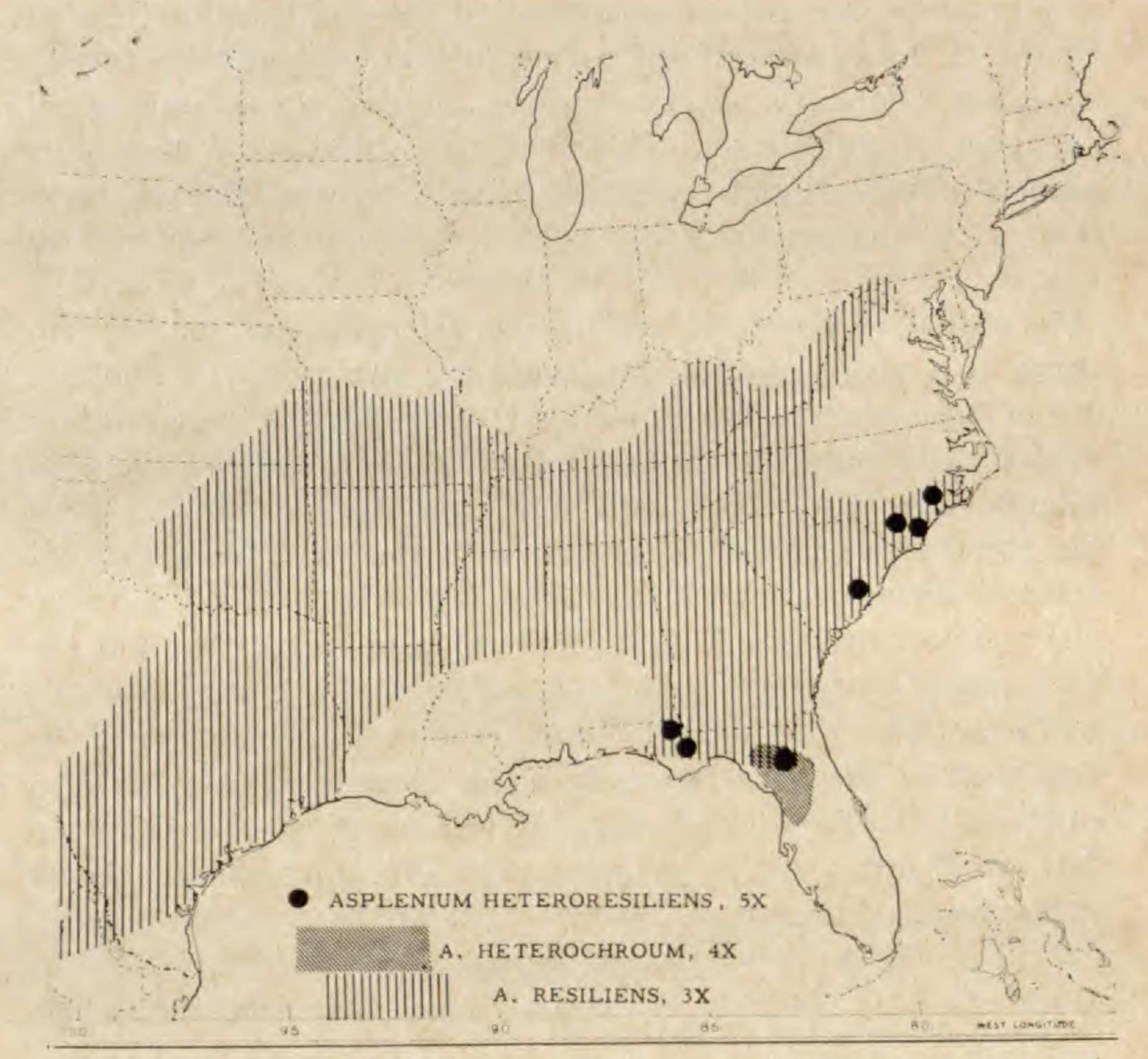


FIG. 1. RANGES OF ASPLENIUM RESILIENS, A. HETEROCHROUM, AND A. HETERORESILIENS, WHICH IS ALSO KNOWN FROM SOUTHEASTERN GEORGIA.

narrowed all appear to be medial. In A. heterochroum the sori are normally medial, lying roughly half-way from the margin to the costa; in A. resiliens the sori tend to be submarginal except in narrowed pinnae. The spores of A. heteroresiliens are not 64 per sporangium as in A. heterochroum, but are usually 32 per sporangium as in A. resiliens. The spores of A. heteroresiliens that are not aborted average larger than those of either other species.

The cytogenetic variations in the Asplenium trichomanes group of spleenworts have been shown to be extensive. The subject is being investigated by Dr. John D. Lovis of the University of Leeds. In the mountains of the southeastern United States, A. trichomanes itself occurs in three sporophytic forms: a sexual diploid, a sterile triploid, and a sexual tetraploid (Wagner, unpublished). The cytological studies of Miss Virginia M. Morzenti and the writer (1962) revealed that A. resiliens is an apogamous fern, with a sporophytic chromosome number of 108 (= 3x), and a gametophytic number of 108; it lacks sexual fertilization. Asplenium heterochroum, on the contrary, is a sexual species; but there are two types in Florida; one of them a tetraploid (2n = 144), and the other a hexaploid (2n = 216). Asplenium heteroresiliens is a pentaploid apogamous fern (in which both "2n" and "n" = 180). Thus the chromosome situation accords with the hypothesis that A. heteroresiliens probably arose from hybridization of a tetraploid, sexual species and a triploid, apogamous species, and the most likely parentage is A. heterochroum (4x form) and A. resiliens (3x). The data to support these statements will be published in the near future by Miss Morzenti. She will also enumerate the known collections of this plant, as shown by the dots in Figure 1 in comparison with the approximate ranges of its presumed ancestors.

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BOTANY DEPARTMENT AND HERBARIUM, UNIVERSITY OF MICHIGAN, ANN ARBOR, MICHIGAN 48104.

An Annotated List of the Pteridophytes of San Luis Obispo County, California

ROBERT F. HOOVER

This list represents a small part of the work on a county flora, which has been in progress for nearly twenty years. Most of the specimens here cited are in the herbarium of the California Academy of Sciences, where most of the preparation of this paper was done. Specimens cited without indication of collector are mine.

San Luis Obispo County is in coastal southern California, above Santa Barbara County. The region is largely one of low mountains, both adjacent to the coast and inland, with peaks rising to approximately 4300 feet. The principal ranges are the Santa Lucia Mountains in the northwest, the La Panza

The officers and staff of the California Academy of Sciences, particularly Mr. John Thomas Howell, Curator of Botany, were most helpful in making facilities available and in various other ways. Thanks are also due my wife for secretarial and other help, not only in preparing this report, but in many phases of the entire project.